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### Deposited in DRO:

07 December 2015

### Version of attached file:

Accepted Version

### Peer-review status of attached file:

Peer-reviewed

### Citation for published item:

Elton, S. (2006) 'Forty years on and still going strong : the use of hominin-cercopithecoid comparisons in palaeoanthropology.', *Journal of the Royal Anthropological Institute.*, 12 (1). pp. 19-38.

### Further information on publisher's website:

<http://dx.doi.org/10.1111/j.1467-9655.2006.00279.x>

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## **40 years on and still going strong: the use of hominin-cercopithecoid comparisons in palaeoanthropology**

### **Abstract**

Hominin-cercopithecoid comparisons have been used in palaeoanthropology for over forty years. Fossil cercopithecoids can be used as a 'control group' to contextualize the adaptations and evolutionary trends of hominins. Observations made on modern cercopithecoids can also be applied to questions about human evolution. This paper reviews the history of hominin-cercopithecoid comparisons, assesses the strengths and weaknesses of cercopithecoids as comparators in studies of human evolution, and uses cercopithecoid models to explore hominin interspecific dynamics. Cercopithecoids appear to be excellent ecological referents, but may be less good when considering the cognitive abilities and cultural adaptations of hominins. Comparison of cercopithecoid and hominin adaptations at Koobi Fora in East Africa indicates that, whereas the cercopithecoids were largely grass or leaf-eating, the hominins occupied a generalist niche, apparently excluding other primate generalist-frugivores. If any of the hominin species at Koobi Fora were sympatric, analogies with modern cercopithecoids suggest that interspecific contact can not be discounted and may even have been beneficial.

### **Introduction**

Palaeoanthropologists reconstruct the biologies and behaviours of hominin species that are, in most cases, extinct. The evidence of past life available from the

palaeontological and archaeological records is fragmentary both at the individual level and at the species level, representing only a very small proportion of total variation.

Observations on modern humans are used in palaeoanthropological reconstruction, through, for example, gatherer-hunter models of resource acquisition in fossil humans (Lee & DeVore 1968; Tanner 1981; Binford 1981). Modern human skeletal material is also used routinely in morphological studies. Since modern human data only provide one perspective on human evolutionary history, non-human primates are also obvious comparators as they are the mammalian group with which modern humans share the greatest number of biological characteristics and the longest evolutionary history (Foley 1987). Primate palaeoanthropological comparators can be chosen either on the basis of ecological similarity or because of close evolutionary relationships. For many palaeoanthropological studies, the great apes are the 'default' comparative sample. Of all the primates, they are the most closely related to humans. They are also big-brained, cognitively sophisticated (Tomasello & Call 1997), have the rudiments of culture (McGrew 1992), and share the orthograde posture of humans, leading to various morphological as well as cognitive similarities.

However, the apes are by no means the only primate comparators available to palaeoanthropologists. Cercopithecids, or Old World monkeys, share a large number of behavioural and ecological features with hominins. Like humans and some earlier hominins, they are extremely successful in terms of both biomass and geographic coverage. Unlike the great apes, they generally respond quickly to habitat change and often co-exist with humans. Opportunistic, eclectic feeding ('omnivory') contributes to

this flexibility. Many cercopithecids are primarily adapted to relatively open habitats, such as grassland and woodland but are also observed using more closed habitats (Rowell 1966). It is increasingly apparent that Plio-Pleistocene hominins may have used a variety of open and closed habitats (Reed 1997; Wolde-Gabriel 2001), so cercopithecids might be more ecologically similar to hominins than are apes. Given these factors, larger numbers of researchers are now using cercopithecoid comparators.

In the first part of this article the history of cercopithecoid models in palaeoanthropology is outlined. The advantages and disadvantages of using cercopithecids in comparative frameworks are explored with an emphasis on their use in ecological and behavioural reconstruction, as a discussion of primate models for human physiology or neurobiology is beyond the scope of this paper. In the second part the ecology and interspecific dynamics of Plio-Pleistocene hominins from East Africa are examined using cercopithecoid referents. The interactions between contemporary species of hominins, cercopithecids, and other large mammals are also considered. This moves away from the traditional use of cercopithecids as referential models, considering them instead alongside hominins as actors in complex ecosystems.

### **The history of cercopithecoid comparisons in human evolution**

Research into chimpanzee ecology and behaviour has a relatively short history, so baboons were the first primates to be used in models of human evolution. Cercopithecoid-hominin comparisons became prominent in the 1960s and enjoyed over a decade of popularity. In the late 1970s and 1980s, they tended to be replaced by ape

models because of the closer evolutionary relationship apes had with humans and also due to increasing knowledge of ape ecology and behaviour (Tanner 1981). However confidence in the hominin-cercopithecoid comparison is currently re-emerging and as it does the range of comparative species grows. Traditionally cercopithecoid models have focused on the larger-bodied, terrestrial baboons (*Papio* subspecies) and the gelada (*Theropithecus*). The relatively small macaques and the forest-living drills, mandrills, and mangabeys only rarely feature in comparisons although the utility of macaques as referents is being recognized (Schillaci & Froehlich 2001). The mainly forest-living, arboreal guenons are also infrequently used, but again, the potential of this group, which also contains terrestrial and semiterrestrial monkeys (Gebo & Sargis 1994), is being recognized, especially for models of human locomotor evolution (Isbell *et al.* 1998; Polk 2004). This represents a significant widening of the hominin-cercopithecoid comparison and shows that comparative taxa should be selected on the basis of the hypothesis to be tested.

Baboons were among the first primates to be observed thoroughly by scientists as their existence in large groups in relatively open habitats made them easy to study (Richard 1985). Data on baboon ecology and sociality were readily available and was probably a factor in the use of baboons in early models of hominin evolution (Tanner 1981). Another was the widespread interest in adaptation to savanna living. It has also been argued that baboons presented an attractive animal model for early humans because of the perceived importance of dominant males (Tanner 1981).

Washburn & Devore (1961) produced the earliest well-cited baboon model, using

baboon field data to contextualize and reconstruct the possible social behaviour of early humans. The differences between modern 'preagricultural' humans and baboons were stressed, with the hominin fossil and archaeological records used to identify the stage in human evolution when hominin behaviour started to become more human-like than like monkeys (or apes). Other research using field observations of modern baboons built on this work to construct models for different aspects of hominin behaviour. Crook & Aldrich-Blake (1968) suggested that the interactions of Old World monkey species might resemble those seen in early hominins under conditions of climatic and environmental change. Rose (1976) examined the circumstances under which the olive baboon used bipedalism and argued that this behaviour could be used as a model for the development of bipedalism in pre-hominins, with feeding acting as a primary selective pressure reinforced by the use of bipedalism in other circumstances, including social interaction. Strum & Mitchell, in a review of papionin models (1987), also used observations of the olive baboon to comment on human predatory behaviour, aggression, dominance, and politics.

Probably the most famous of all hominin-cercopithecoid comparisons, Jolly's (1970) 'seed-eating hypothesis', broadened the taxa used as comparators, specifically introducing *Theropithecus* as a model primate. Published in *Man*, a former incarnation of this journal, 'the seed eaters' has been an enduring and influential model, at times misunderstood and criticized (Jolly, 2001) but nonetheless stimulating debate and setting standards for future models. Through detailed study of the morphology of various primates, including *H. sapiens*, *T. gelada*, *Pan*, and *Papio*, it provided a plausible

basis for hominin differentiation from other closely-related species. The similarities between various adaptations evident in australopiths and the graminivorous *Theropithecus gelada*, including open-country habitat, opposability of thumb and index finger, and features of the jaw and teeth, were seen as evidence for an ancestral diet of small, hard-object feeding in hominins that precipitated upright stance and bipedal locomotion. The seed-eating hypothesis was important, not only in that it addressed fundamental questions about the origin and early evolution of humans but also because it emphasised that humans were likely to have been subject to at least some of the selection pressures operating to cause evolutionary change in other Plio-Pleistocene mammals.

After the 'seed-eating hypothesis', *Theropithecus* became a popular comparator. Wrangham (1980) compared and contrasted *Theropithecus* and hominin locomotor behaviour to develop a functional hypothesis for the evolution of hominin bipedalism. The contrasting dietary responses of *Theropithecus* and hominins to changing habitats were explored by Dunbar (1983). Foley (1984, 1993) took this further, examining the broader patterns of evolution in robust and gracile hominins and theropiths in the context of environmental and climatic change during the Plio-Pleistocene. Foley's work highlighted the shared environment of Plio-Pleistocene hominins and cercopithecids, stressing the importance of viewing human evolution from the perspective of the wider mammalian community. Using this idea, Elton *et al.* (2001) compared trends in theropith endocranial volumes over the course of the Plio-Pleistocene with trends in the *Paranthropus* and *Homo* lineages. *Theropithecus* social behaviour has also been used in at

least one evolutionary scenario, with the relatively complex vocalizations used by *T. gelada* to convey information and emotion suggested as a model for the early stages of hominin language (Aiello and Dunbar 1993).

The past decade has seen a resurgence in the popularity of the hominin-cercopithecoid comparison, with greater diversity of taxa used in the models. These comparisons have been fairly wide, including brain size evolution, biomechanics, and speciation. Isbell *et al.* (1998) used data from modern patas monkeys and other guenons to formulate a model accounting for the selective pressures that acted on hominins during the Plio-Pleistocene and which resulted in the long leg length of *H. ergaster*. In another locomotor study, the influence of limb proportions and body size on primate locomotor kinematics were examined (Polk 2004). Experimental data from patas monkeys and baboons were used to model the effects of differing limb proportions and body sizes on hominin locomotion. Patas monkeys, with long limbs and a high crural index (relative length of the tibia and femur), and baboons, with shorter limbs and a lower crural index, were argued to be good models for modern humans and Neanderthals respectively, and their differences were seen to reflect those of *Homo ergaster* versus the australopiths. Polk's (2004) study extended the utility of hominin-cercopithecoid comparisons in an important direction, establishing that for certain studies quadrupedal non-orthograde species could be used to test hypotheses relating to the biomechanics of bipedal locomotion.

Speciation and taxonomy have also been the subject of hominin-cercopithecoid comparisons. Several cercopithecoid taxa that are morphologically distinct hybridise in



the wild, making them appropriate models for modern humans and Neanderthals, two other primate taxa that are morphologically distinguishable but may have interbred (Schillaci & Froehlich 2001). Evidence from hybridising and non-interbreeding Sulawesi macaques was used to show that Neanderthals are a species in their own right, probably replaced by modern humans rather than being 'absorbed' through hybridisation (Schillaci & Froehlich 2001). Harvati *et al.* (2004) tested this idea further, using a larger catarrhine sample, with apes as phylogenetic comparators and papionins as ecological referents, again coming to the conclusion that Neanderthals were a separate species. Jolly (2001), using macaques and baboons (likely to be phylogenetic species but biological subspecies), suggested that replacement in Europe occurred via a moving hybrid zone between different hominin 'species'. This idea, contrasting with other cercopithecoid-hominin comparisons, needs testing further, but the baboon analogy, as Jolly (2001) points out, certainly shows that there is probably much more to hominin species relationships and speciation than can be discerned from the evidence in the fossil record alone.

The hominin-cercopithecoid comparison has survived for over forty years and it is inevitable that as palaeoanthropological knowledge widens some of the scenarios presented are challenged. For example, relatively recent data on early hominin diet and foraging strategy indicating that meat-eating may have been part of australopith feeding behaviour (Sponheimer & Lee-Thorp 1999) casts 'the seed-eaters' in a different light. However, challenges to models based on cercopithecoid comparators do not invalidate the basis of such comparisons.

Many of the main preoccupations of palaeoanthropology – bipedalism, diet, brain evolution, social organization, origins of language, speciation, and taxonomy – have been explored in at least one cercopithecoid-hominin comparison. The longevity of the hominin-cercopithecoid comparison makes it possible to track whether its use reflects the changing preoccupations of palaeoanthropology.

One topic that never goes out of fashion is hominin locomotion. The origins of bipedalism and the locomotor behaviours of hominins are revisited frequently, and this is reflected in the continuing popularity of using hominin-cercopithecoid comparisons in locomotor studies. Washburn & DeVore (1961) explained the relatively altricial status of the human neonate by contrasting the demands of quadrupedal locomotion with those of bipedalism. Rose (1976) and Wrangham (1980) sought to explain the origins of human bipedalism using evidence from the circumstances under which cercopithecoids use bipedalism. Isbell *et al.* (1998) used a guenon analogy to provide valuable insight into the development of bipedalism after 2 Ma (two million years ago). Most recently, Polk (2004) used experimental data from cercopithecoids to address the biomechanics of skeletal proportions in different hominins.

Diet is also an enduring theme in the palaeoanthropological literature and, unsurprisingly, a number of the earlier hominin-cercopithecoid comparisons – most famously ‘the seed-eaters’ (Jolly 1970) but also Washburn & DeVore (1961) and Dunbar (1983) – considered hominin diet. However, dietary models are not as prominent as those based on locomotion. Cercopithecoids, especially those such as baboons and macaques that have eclectic feeding behaviours, have huge potential to contextualise

hominin diet (Lee-Thorp *et al.* 2003) and, with the widespread adoption of scientific archaeological techniques for investigating diets, this is likely to be a 'growth area' in future hominin-cercopithecoid comparisons.

Discoveries of new fossils to add to the human evolutionary tree have meant that increasing numbers of hominin species are recognized. Since 1994, fossil discoveries have led to the description of at least nine new hominin species (White *et al.* 1994; Leakey *et al.* 1995; Carbonell *et al.* 1995; Brunet *et al.* 1996; Asfaw *et al.* 1999; Leakey *et al.* 2001; Senut *et al.* 2001; Brunet *et al.* 2002; Brown *et al.* 2004), so currently there is great interest in hominin speciation and species concepts. Analogy with modern cercopithecoids has been one response to the challenge of exploring taxonomy and speciation in human evolutionary history (Schillaci & Froehlich 2001; Jolly 2001; Harvati *et al.* 2004), a new application of the hominin-cercopithecoid comparison.

Obvious omissions in the use of cercopithecoid models centre on tool-use and cognition. However, given the ecological and population similarities of hominins and cercopithecoids, there are less obvious gaps. As well as the under-exploitation of the cercopithecoid comparison to explore hominin dietary evolution, few studies have used the behaviour of extant cercopithecoids to construct scenarios for the interactions of sympatric early hominin species. Crook & Aldrich Blake (1968) made preliminary comments on the value of using cercopithecoids in this way, and further observations are made later in this article. Consideration of the role of hominins in the wider primate community has also received relatively little attention other than a small body of research concerning hominin predation on large Pleistocene monkeys (Shipman *et al.*

1981). The inter-specific dynamics of hominins are thus also considered further below.

### **Choosing a comparative sample: the advantages and disadvantages of cercopithecoid models**

It would be naïve to suggest that any one group of modern primates, be it apes, monkeys or humans, is directly analogous to extinct hominins. However, when thinking about appropriate primate models, care must be taken to ensure that the baby isn't thrown out with the bath-water; imperfect comparators for which the limitations are known are clearly better than no comparators at all. The choice of a comparative sample is not an inconsequential decision as it influences the comparisons made and the results that emerge from the work. Decisions on which primate group to use must be driven by the question being asked, or the hypothesis to be tested, and there must be careful consideration of a sample's advantages, disadvantages and limitations.

Fossil cercopithecoids can be used as a 'control group' to assess patterns in human evolution. Common evolutionary trajectories can be revealed and important differences highlighted from which it might be possible to infer evolutionary processes. Elton *et al.*'s (2001) research into brain size trends in Pleistocene *Theropithecus*, *Homo* and *Paranthropus* lineages is an example of a 'control group' study. Cercopithecoids, as large-bodied primates, are uniquely fitted to this type of approach. In the absence of apes from the Pliocene and Pleistocene fossil records, cercopithecoids are the animals with the closest evolutionary relationship to hominins. At African Plio-Pleistocene palaeontological and archaeological sites, cercopithecoids are often found in the same localities and in the same

horizons as hominin fossils or archaeology (Foley 1993). Hominins and cercopithecids both underwent an extensive adaptive radiation during the Plio-Pleistocene, having been represented by only a small number of species in the late Miocene. Some fossil monkey genera, in particular *Theropithecus*, but also *Parapapio* and *Cercopithecoides*, had similar biogeographic ranges to early hominins (Strait & Wood 1999; Elton 2000). Plio-Pleistocene hominins and cercopithecids also had convergent body masses with some *Theropithecus oswaldi* specimens attaining body masses in excess of 60kg (Jolly 1972; Krentz, 1993; Delson *et al.*, 2000), easily within the range found in Plio-Pleistocene hominins (Wood & Collard 1999). Thus, hominins and cercopithecids may have been subject to similar selection pressures, both abiotic (for example, climate change) and biotic (such as predation).

Alternatively, extant cercopithecids can be used to explore the range of responses to particular environmental conditions or to examine selective pressures that may have acted on hominins. Isbell *et al.*'s (1998) use of patas monkeys is a good example of this. Another way to think about the utility of modern monkeys analogies is with the example of feeding behaviour. Like modern humans (Ulijaszek 2002), and many Pliocene and Pleistocene hominins whose diets probably included a mixture of plant foods, insects and other fauna (Wood & Strait 2004; Plummer 2004; Peters & Vogel 2005), modern baboons and macaques are eclectic feeders ('omnivores'). Through examining the circumstances that alter feeding behaviours in extant cercopithecids, it may be possible to make more accurate assessments of how hominin diets varied under different environmental conditions. Combining baboons as analogues for tropical African

hominins and macaques for higher-latitude, cold adapted hominins could give additional depth to this type of work, and it is the ecological similarity of hominins and cercopithecids that makes such comparisons feasible. Indeed, it has been argued that the similarities in cercopithecoid and hominin distributions and diets make cercopithecids excellent modern primate comparators in studies of hominin ecology (Aiello *et al.* 2000; Lee-Thorp *et al.* 2003).

Given the compelling ecological and evolutionary similarities between cercopithecids and hominins, it may be tempting for the 'cercopithecophile' to assume that the advantages of cercopithecoid models outweigh the disadvantages in most circumstances. However, denying the potential weaknesses of cercopithecoid comparators limits their utility. Criticisms of cercopithecoid models centre on three main areas: the notion that 'savanna models' are outdated, the distance of the evolutionary relationship between hominins and cercopithecids, and the greater cognitive similarities of apes and hominins (Tanner 1981).

An ever-expanding body of evidence indicates that early hominin environments were not uniform, comprising closed as well as more open habitats (Reed 1997; Wolde Gabriel *et al.* 2001). Some initial justification for the hominin-cercopithecoid comparison relied on similarities in open habitat adaptation but, as the earliest stages of hominin evolution did not occur exclusively, if at all, on open savanna grasslands, there has been much debate over the validity of savanna hypotheses for human evolution (Potts 1998). Early hominins may not have been subject to the same pressures as those modern baboon troops that exist mainly in open grassland. However, baboons, as well as many

other cercopithecids, are highly flexible and able to survive in a wide range of habitats including those experiencing rapid change, so may in fact be excellent models for early hominins in mosaic and changing habitats. The limitations of savanna models do not invalidate the basis of the hominin-cercopithecoid comparison, but the cercopithecoid species used must be appropriate. *Theropithecus gelada*, with its extreme specialisms for grass-eating and open-country living (Napier & Napier 1967), for example, would be a poor analogue in studies of ecological flexibility.

Humans and great apes have a very close evolutionary relationship, with chimpanzees and humans likely to be most closely related to each other (Ruvolo 1997). The behavioural and morphological similarities between humans and great apes are undeniable. Compared to monkeys, apes have long periods of maturation and fewer offspring demonstrating their closer phylogenetic relationship to humans through more similar life histories (Tanner 1981). Thus, social learning models in hominins may benefit from being based on ape rather than monkey comparators (Tanner, 1981). Social system is closely tied to phylogeny, so apes may be the most appropriate starting point for the reconstruction of core social systems in hominins (Foley & Lee 1989). Craniodentally, hominins are much more similar to apes than to the bilophodont cercopithecids of which several genera have 'dog-like' faces. Postcranially, humans and apes are orthograde whereas monkeys are pronograde. In simple, referential (*sensu* Tooby & DeVore 1987) models of morphology, therefore, apes will probably be a better choice of comparative sample than monkeys. However, work on intraspecific variation in primates and its implication for hominin species diversity (Schillaci & Froehlich 2001; Harvati *et al.* 2004)

demonstrates that close phylogenetic ties and morphological similarities are less important if direct comparisons are unnecessary and the aim is to understand broad principles. Reinforcing this, Polk (2004) demonstrated that pronograde quadrupeds can be used as analogues for bipedal hominins provided that the biomechanics underpinning morphology and function in the taxa are similar.

Apes have better-developed cognitive abilities than monkeys (Tomasello & Call 1997) and are unquestionably the most appropriate comparators for hominins in terms of cognition and assessment of complex 'cultural' behaviour. Martin (1993) argued that the relatively small brains of *Theropithecus* species make them – and possibly by extension other cercopithecids – poor comparators for hominins. This is clearly not universally true, but is reasonable when considering cognition and cultural behaviour. Cercopithecids are highly intelligent, and there are widely-cited examples of monkey 'culture', best known from Japanese macaques (Imanishi 1957). However, although some Neotropical primates have quite complex tool use (Phillips 1998), Old World monkeys lack the material culture found in chimpanzees (McGrew 1992) and recently discovered in orangutans (van Shaik *et al.* 2003). A great deal of information about chimpanzee tool use and manufacture is available, and this has been used to great effect in models of human behavioural evolution (see McGrew 1992 for an extensive review). Although great apes are the obvious direct referents in studies of hominin cognition and cultural behaviour, the small number of extant apes makes detection of broad trends in brain evolution difficult. In a number of studies (e.g. Aiello & Dunbar 1993) predictions for hominin behaviour and cognitive ability have thus been based on a catarrhine



(cercopithecoid and hominoid) sample.

Whatever primate comparator is chosen, all models are approximate and cannot reveal absolute truths about human evolutionary history. However, by exploring the principles that underlie certain types of behaviours in modern primates, inferences about what was possible in hominins under specific conditions can be made (Strum and Mitchell 1987). In some cases, the study of apes will provide the most appropriate baseline, but in others certain cercopithecoid species will be more informative. The most recent referential models and analogies from modern cercopithecoids to hominins (for example, Isbell *et al.* 1998; Jolly 2001; Polk 2004) have avoided the trap of over-simplification by identifying the underlying biomechanical, ecological, or evolutionary principles that influence morphology and behaviour. They show the sophisticated approach to the hominin-cercopithecoid comparison advocated by Strum & Mitchell (1987). Comparative contexts can go further, however, than simply using modern taxa. By comparing the responses of contemporary fossil taxa to shared environmental conditions, distinctive behavioural and biological features can be identified; if such features are not found, general models of evolution can be constructed (Finlayson 2004). Now that analogies using modern animals have matured, new hominin-cercopithecoid comparisons might well focus on contemporary interactions between taxa, and 'control group' studies of the type illustrated below.

**Competition and interaction: reconstructions of hominin interspecific dynamics using cercopithecoid comparators**

Plio-Pleistocene hominins lived within an evolving ecological community comprising multiple vertebrate species, a diverse invertebrate fauna, and many plant taxa. In some Plio-Pleistocene deposits, such as those at Koobi Fora in East Africa, several hominin species are found (Turner *et al.* 1999). Thus, hominins may have faced interspecific competition from other hominins as well as from the rest of their community. Much has been made of the hominin role within the large carnivore guild (Lewis 1997; Plummer 2004), but less is understood about the interactions between hominins and other large-bodied mammals, including the cercopithecids. There has also been remarkably little consideration of how contemporaneous (and therefore possibly sympatric) hominin species may have interacted with one another. Here, the palaeobiology of cercopithecids from Koobi Fora between 2 and 1.64 million years ago is used to contextualise the inter-specific dynamics of hominins found in the same horizons, focusing on habitat use and dietary behaviour. Evidence from modern cercopithecids is then used to reconstruct possible inter-specific competition and interaction within the hominins themselves.

### **Fossil Cercopithecid 'Control Groups': Niche Separation In Koobi Fora Primates**

In the Upper Burgi and KBS Members of Koobi Fora, two consecutive fossil-rich strata dated to between 2 and 1.64 million years ago (Brown & Feibel 1991), up to four hominin species – *H. habilis*, *H. rudolfensis*, *P. boisei* and *H. ergaster* – have been identified (Turner *et al.* 1999; Wood & Strait, 2004). The body masses of the hominin species found at Koobi Fora probably ranged from around 34kg to 58 kg (Wood & Collard, 1999).

Direct data on the diets of hominin specimens found at Koobi Fora are scarce but a number of lines of evidence indicate that *Paranthropus* and early *Homo* were dietary generalists, incorporating foods derived from C<sub>3</sub> plants (such as trees, shrubs and temperate grasses) as well as C<sub>4</sub> plants (mainly tropical and sub-tropical grasses) in their diets (Wood & Strait 2004; Peters & Vogel 2005). Dietary components might have included vertebrates, invertebrates, fruits and tubers (Wood & Strait 2004; Plummer 2004; Peters & Vogel 2005). Despite its reputation as a 'chewing machine', consuming fibrous, low-quality foods (Robinson 1954), *Paranthropus* is unlikely to have included leaves in its diet as its molar occlusal surfaces lack shearing crests (Teaford & Ungar 2000). The primary locomotor mode of the Koobi Fora hominins was terrestrial bipedalism, but *H. habilis* and *P. boisei* might also have been capable of exploiting arboreal substrates (Wood & Collard 1999). The palaeoenvironment of the Upper Burgi Member has been reconstructed as fairly wooded and wet, with the younger KBS Member showing evidence of more open habitats (Reed 1997). It has been argued that none of the hominin species found in the Upper Burgi and KBS Members had a strong habitat preference (Wood & Strait 2004), although *H. ergaster* may have preferentially inhabited the more open areas (Reed 1997). The hominins found in the Upper Burgi and KBS Members of Koobi Fora can therefore be reconstructed as generalists, with broad diets and the ability to exploit a variety of habitats.

Several cercopithecids are known from the Upper Burgi and KBS Members at Koobi Fora, including *Theropithecus oswaldi*, *Theropithecus* sp. indet, *Cercopithecoides williamsi*, *C. kimuei*, *Rhinocolobus turkanaensis* and *Cercopithecus* sp. indet (Elton 2000).

*Cercocebus* and *Papio* may also be represented (Turner *et al.* 1999) but these taxa are rare in the fossil record of East Africa at this time and many of the specimens are fragmentary (Szalay & Delson 1979). Most of the cercopithecids at Koobi Fora were relatively large-bodied, and overlapped in size with the hominins (Figure 1). *C. kimuei* has an estimated mass of 51kg (Delson *et al.* 2000) and *T. oswaldi* is estimated at 50kg (Delson *et al.* 2000). *R. turkanaensis* and *C. williamsi* are smaller, at 31kg and 25kg respectively (Delson *et al.* 2000). There are no mass estimates for indeterminate *Theropithecus* species but femoral head diameters, a cercopithecoid body mass proxy (Elton & Bishop 2004), in the specimens from the Upper Burgi and KBS Members lie within the range of diameters found in *T. oswaldi* and *C. williamsi* (Elton, unpublished data). This indicates that the *Theropithecus* specimens were similar in size to these animals. There are no accurate body mass estimates for fossil *Cercopithecus* but the femoral head diameter of the *Cercopithecus* specimen KNM-ER 85 measures 12.3mm (Elton, unpublished data), very close to the mean femoral head diameter ( $12.7 \pm 1.6$  mm) of a pooled sample of modern *C. aethiops* and *C. neglectus* (Elton 2000). This suggests that KNM-ER 85 was of a similar body mass to modern *Cercopithecus*; based on data from Smith & Jungers (1997) a conservative estimate of its mass would be 5kg.

FIGURE 1 HERE

Ecomorphic analysis of the proximal and distal humerus, the proximal ulna, and the distal femur (with the methods drawn from Elton 2001, 2002) indicates that Koobi Fora

cercopithecids used a variety of habitats, from forest to grassland (Figure 2). The majority appear to have favoured relatively open habitats, possibly woodland or wooded grassland, with this becoming more marked in the KBS Member. This fits interpretations of the Koobi Fora palaeoenvironment as a whole (Reed 1997). There are no data for the habitat preferences and locomotor strategies of *Papio* and *Cercocebus* at Koobi Fora. However, *T. oswaldi* probably inhabited open areas, being primarily terrestrial but using trees when available in a manner similar to extant common baboons (Elton 2002). A similar habitat preference was also observed in most of the specimens assigned to *Theropithecus* sp. indet, as well as in *Cercopithecus*, represented by a single specimen that was likely to have used its habitat in a way similar to that seen in the modern vervet monkey (Elton 2000), and in *Cercopithecoides williamsi* (Elton 2000, 2001). The terrestriality of *C. williamsi*, a colobine, has also been noted in previous studies (Birchette 1982; Ciochon 1993). In contrast, another Koobi Fora colobine, *R. turkanaensis*, was very likely to have inhabited a closed, forested habitat and used predominantly arboreal locomotion (Elton 2000). This reconstruction is supported by the notion that *Rhinocolobus* was probably the most arboreal of all the Pliocene colobines from East Africa (Delson *et al.*, 2000). The locomotor strategy of a third colobine, and the largest monkey at Koobi Fora around 2 million years ago, *C. kimuei*, is unknown, as postcranial remains assigned to the species are rare and fragmentary, but it is associated in the fossil record of East Africa as a whole both with woodland and with grassland habitats (Frost *et al.* 2003). The range of cercopithecoid habitat preferences and locomotor strategies at Koobi Fora demonstrates that a number of habitats suitable for exploitation by

large-bodied primates, including hominins, existed. The decrease of forest-living arboreal cercopithecids in the more recent Koobi Fora deposits, a pattern that is also observed in fossil cercopithecids from East Africa as a whole (Figure 3), appears to coincide with the rise of the more terrestrial *H. ergaster* / *H. erectus*.

FIGURES 2 & 3 HERE

Several cercopithecoid species have been found in the same horizon and collection area as hominin fossils or evidence for hominin activity (Elton 2000). Thus it is possible that at least some cercopithecoid taxa would have been sympatric with hominin species, although if the environment was made up of fragmented, mosaic habitats, true sympatry might not have occurred. Judging whether or not fossil species were sympatric is problematic since fossil deposits are often time and space averaged, but the fact that several hominin and cercopithecoid species are found associated in the fossil record over a long period of time makes some degree of sympatry possible. In addition, cut marks from stone tools on the bones of *T. oswaldi* at Olorgesailie (Shipman *et al.* 1981) point to a degree of interaction and potential sympatry between a hominin species – probably *H. ergaster* / *H. erectus* – and *Theropithecus*. Despite the suggestion that the hominin species found at Koobi Fora do not appear to have strong habitat preferences (Wood & Strait 2004), it is highly likely that they would have preferentially used more open, wooded habitats over closed, densely forested areas. These are also the habitats apparently favoured by the cercopithecids at Koobi Fora. Thus, although the presence of sympatric

large-bodied primate species cannot be proved conclusively, it cannot be discounted. If some cercopithecoid and hominid species at Koobi Fora were sympatric, a degree of niche partitioning would have been necessary to reduce competition for resources, particularly given the convergence of body masses. It is also very probable that hominids and other large-bodied primates were sympatric with other mammals, so it is plausible that the Koobi Fora primates, including hominids, had to compete with other mammals and birds for access to plant (and possibly invertebrate) resources, and that hominids competed with carnivores for vertebrate prey.

It is fairly certain that *Theropithecus oswaldi* was a grass-eater (Jolly 1972), possibly supplementing with leaves (Teaford 1993) or even fruit at Koobi Fora (Benefit 1999), but the dietary strategies of the other Koobi Fora cercopithecoids are not as well understood. *C. kimuei* may have incorporated roughly equal proportions of fruit and leaves into its diet, with the other colobines (*C. williamsi* and *R. turkanaensis*) eating a greater proportion of leaves (Benefit 1999). Palaeodietary adaptations of *Cercopithecus*, *Cercocebus* and *Papio* in East Africa are largely unknown, but *Papio robinsoni* from southern Africa was probably a C<sub>3</sub> browser (Lee-Thorp *et al.* 1989), so *Papio* from Koobi Fora may have been a generalist frugivore. *Cercocebus* from Koobi Fora was predicted to be a frugivore on the basis of tooth morphology (Benefit 1999). Based on the ecology of modern guenons, *Cercopithecus* at Koobi Fora may also have been frugivorous, although the diets of fossil animals may not be directly analogous to those of their closest living relatives (Sponheimer & Lee-Thorp 1999). *Papio* and *Cercocebus* are rare at Koobi Fora, and *Cercopithecus* is not as abundant as *Theropithecus* and the colobines. From the evidence

available, it appears that most cercopithecids and hominins were not competing directly for foodstuffs as the majority of the Koobi Fora monkeys apparently had diets based on leaves/grass in contrast to the more eclectic diets of hominins. Dunbar (1983) suggested that a move towards graminivory in cercopithecids occurred because of Plio-Pleistocene climate change. The presence of folivores and graminivores in the mosaic, fairly wet, wooded habitat of Koobi Fora around 2 Ma suggests that this was not the case, with a dependence on leaves and grass instead occurring because large-bodied primates occupying similar habitats needed to partition niches.

Other large-bodied mammals that may have competed with hominins for resources at Koobi Fora include suids (pigs), often thought of as 'omnivores', and the carnivorous big cats, hyenas, and canids. Three suid species - *Notochoerus scotti*, *Kolpochoerus limnetes* and *Metridiochoerus andrewsi* - are present in both the Upper Burgi and the KBS Members of Koobi Fora with a further species, *M. compactus*, found in the KBS Member (Turner *et al.* 1999). Dietary data for *M. compactus* are not available but stable carbon isotope analysis of tooth enamel from the other Koobi Fora pigs indicates that they all had diets based on C<sub>4</sub> tropical grasses (Bishop *et al.* 1999). Few postcrania assigned specifically to these taxa are known, but ecomorphic analysis of a partial *K. limnetes* skeleton indicates that it had a preference for intermediate (bushland) habitats (Bishop *et al.* 1999). This pattern was also evident in Koobi Fora suid specimens without a taxonomic identification, with a high proportion assigned to closed and intermediate habitats (Bishop 1994). Pigs living in these habitats could have had access to tropical grasses because C<sub>4</sub> plants may have been a significant component of bushland flora and



also would have occurred in disturbed parts of forests (Bishop *et al.* 1999). It appears that by exploiting only C<sub>4</sub> foods the Koobi Fora pigs may have been occupying different dietary niches to those of the hominins.

Hominins would have faced competition from carnivores for meat (Plummer 2004). Although caution regarding sympatry is as applicable to hominins and carnivores as it is to cercopithecids or pigs, sympatry between some carnivores and hominins at Koobi Fora is likely. In the Upper Burgi Member, five carnivore taxa – *Homotherium crenatidens*, *Megantereon cultridens* (sabretooth cats), *Dinofelis barlowi* ('false' sabretooth), and the hyenas *Crocuta crocuta* and *Hyaena hyaena* – are found (Turner *et al.* 1999). All these species apart from *D. barlowi* are present in the KBS Member from which *Canis mesomelas* has also been recorded. It has been suggested that hominins formed part of the East African carnivore guild (Lewis 1997). Access to meat is highly competitive, with body mass an important determinant of rank within guilds (Plummer 2004). The body masses of the Koobi Fora carnivores ranged from 30kg to 170kg (Plummer 2004), overlapping with the hominins that are nonetheless found near the bottom of the distribution (Figure 1). A number of studies suggest that meat formed part of Plio-Pleistocene hominin diets and it is possible, but as yet unconfirmed, that the smaller hominins, such as *H. habilis*, used grouping behaviour to compete with carnivores (Plummer 2004). However, the ancestral diet of hominins, as primates, would be plant-based (Milton 1999) and it is likely that plant foods were integral to the diets of the Koobi Fora hominins. Eclectic, generalist feeding appears to be part of hominin heritage (Teaford & Ungar 2000) that may have been worth maintaining as an important adaptive

strategy because of the rank of Plio-Pleistocene hominins in the predator guild.

The ecological similarities between hominins and cercopithecids or hominins and suids are often cited as justification for their use as comparators (Bishop 1994; Elton 2000). Although 'omnivory' is clearly evident in some suid and cercopithecoid species, comparison of the probable diets of Koobi Fora monkeys, pigs, and hominins suggests that hominins, rather than cercopithecids or suids, were filling the generalist niche at Koobi Fora (Figure 4). The most prominent cercopithecoid genus at Koobi Fora, *Theropithecus*, very probably had a grass-dominated diet (Jolly 1972). Several colobine taxa were also present at Koobi Fora, and it appears from their dental morphology that leaves were an important foodstuff (Benefit 1999). Since food limits primate densities (Waser 1987), the poor representation of the cercopithecids that were most likely to be frugivore-generalists could indicate that one or more of the Koobi Fora hominins were highly successful in this niche. This is reinforced by the apparent absence of pigs with a mixed C<sub>3</sub>/C<sub>4</sub> diet. Clearly, more extensive direct study of the diets of different mammals, including hominins, at Koobi Fora is needed before the patterns of niche differentiation suggested here can be confirmed. However, a number of lines of evidence indicate that Plio-Pleistocene hominins had a varied diet, and there is no reason to suppose that the Koobi Fora hominins were any different. Lack of dietary specialism in the Koobi Fora hominins may have minimized competition between them and other large-bodied mammals and allowed the earlier hominins, such as *H. habilis*, to exist as lower-ranked predators.

FIGURE 4 HERE

By putting hominin palaeobiology into the context of the adaptations of contemporaneous mammals likely to have been potential competitors, a broader picture of hominin evolutionary trends can be constructed. Whether or not hominins adapted differently to other mammals under similar circumstances can therefore be assessed. In this case, the cercopithecoid 'control group' indicated that, at Koobi Fora at least, generalist, eclectic feeding was not a common response of all large-bodied primates to mosaic and possibly rapidly changing environments. Thus, without cercopithecoids and other mammals to provide context, our interpretations of human evolutionary history would be much less detailed.

### **Modern Cercopithecoid Analogues: Interspecific Interactions In The Koobi Fora Hominins**

The hominins represented in the fossil record of the Upper Burgi and KBS Members are sufficiently morphologically different to assign to four separate species (Wood 1991). Given that all the hominin species found at Koobi Fora were likely to have been generalists (Wood & Strait 2004), competition **would** have occurred if any were sympatric. Observations on modern animals indicate that where several primate species are sympatric, home ranges are often larger (Waser 1987). Hominins may therefore have used differences in ranging behaviour to help minimize competition, and the hypothesized increased home range area for *Homo ergaster* (Isbell *et al.* 1998) may have been a useful behavioural mechanism in areas with multiple hominin species. Other

aspects of behavioural difference may also have reduced inter-specific competition. Species-specific difference in social organisation has been observed in modern cercopithecoid interaction areas (Crook & Aldrich-Blake 1968), so group structure and mating system, argued to have been different in *Homo* and *Paranthropus* (Foley & Lee 1989), may have helped hominins use the shared environment in different ways. This notwithstanding, interactions between different modern primate species are relatively common (Waser 1987) so regular inter-specific contact between hominin species at Koobi Fora cannot be ruled out. Due to the difficulties of assessing such behaviour from the fossil record, very few studies have considered how different hominin species may have competed or interacted but, as indicated by Crook & Aldrich-Blake (1968), modern cercopithecoids may be appropriate models.

Interactions between different modern cercopithecoid species, and between monkeys and apes, have been observed in many regions of Africa. Forest-living guenons aggregate in mixed-species groups that offer access to resources (Cords 1987) and protection from predation (Gautier-Hion 1988). Monkeys that are more terrestrial, including baboons, vervets and patas, often interact in areas where distinct habitats meet (Crook & Aldrich-Blake 1968). If the Koobi Fora hominins were sympatric, and if *Homo ergaster* preferentially inhabited the more open areas (Reed 1997), different species might have come into contact in transition zones where one habitat gave way to another rather than existing in the mixed-species groups that most often occur in forest-living arboreal primates. Along with competition for food, the costs associated with contact in hominins may have included aggressive interactions, observed between some monkey species

(Waser 1987). However, interspecific aggression in modern ground-living primates from Ethiopia was shown to be low (Crook & Aldrich-Blake 1968) and this is also the case in many other primate groups (Waser 1987). Contact may have brought benefits, including access to food normally unavailable to one of the species, an important aspect of association in modern cercopithecids (Waser 1987). For example, guenons have been observed foraging on fruit leftovers that were initially processed by the larger, heavier-jawed mangabeys (Waser 1987). Dietary breadth may have been facilitated in *Paranthropus* through dental and gnathic adaptations and in *Homo* through cultural innovation (Wood & Strait 2004) so different hominin species may have had differential access to certain resources (Peters & Vogel 2005). It is possible that *Paranthropus*, recently argued to have been an unlikely maker of Oldowan tools (Plummer 2004), may have widened its access to foods that needed complex processing through association with tool-using hominins, or that gracile hominins associated with *Paranthropus* may have behaved like the guenons that follow mangabeys.

The scenarios presented here represent a first attempt to reconstruct the possible inter-specific dynamics of tropical Plio-Pleistocene hominins using modern African cercopithecids as analogues. This work can be extended and refined by performing detailed analysis of how the behaviours of modern cercopithecids alter in different environments and of how ecology influences species interactions. This would lead to more sophisticated models for early hominin behavioural ecology. With increasing amounts of data on hominin environments and diets available for use in such models, this, along with control group studies, is likely to be a fruitful area for the next

generation of hominin-cercopithecoid comparisons.

## **Summary and Conclusions**

Cercopithecoid models have been used in palaeoanthropology for over forty years. Their popularity has fluctuated but the recent proliferation of cercopithecoid-based studies shows their strength and breadth. Cercopithecoids can be used to shed light on human evolution in two ways. The first is through the use of fossil cercopithecoids as a 'control group' contextualising the adaptations and evolutionary trends of hominins found at similar times and in similar places. In the second, observations made on modern cercopithecoids are applied to questions in human evolution. In this paper both approaches were used in a preliminary examination of inter-specific interactions and dynamics at one of the best known Plio-Pleistocene hominin localities, Koobi Fora in East Africa. Comparison of the probable dietary strategies of hominins and cercopithecoids found in the same horizons indicates that niche partitioning probably occurred in the large-bodied Koobi Fora primates, with generalist hominins alongside graminivorous and folivorous cercopithecoids. Analogy with modern cercopithecoids suggests that if any of the Koobi Fora hominin species were sympatric, contact in areas of habitat transition would be more likely than frequent multi-species aggregations. Interaction may have been beneficial, widening access to resources. The conclusions from the new hominin-cercopithecoid comparisons presented in this paper are necessarily tentative. Nonetheless, they, along with the other examples of cercopithecoid comparisons discussed in this paper, show that examining hominin adaptations in wider

ecological contexts – based both on modern and fossil cercopithecids - can give useful insights into the patterns and processes of human evolutionary history.

### **Acknowledgements**

The research on which this paper was based was funded initially by The Wellcome Trust Bioarchaeology Panel and is currently funded by the Leverhulme Trust. I was generously allowed access to the fossil collections held in The National Museums of Kenya and the Natural History Museum London. I thank them and also the many museums that granted access to modern collections. I am grateful to Rob Foley, Laura Bishop and Bernard Wood for introducing me to the concept of the cercopithecoid-hominin comparison and to Hannah O'Regan for discussing some of the ideas presented here with me. Three anonymous reviewers made useful comments, and I thank them for these. Thanks also to the SE541 Evolution of Hominin Behaviour undergraduate class at the University of Kent which – way back in the mists of time – enthusiastically criticized an earlier version of this paper.

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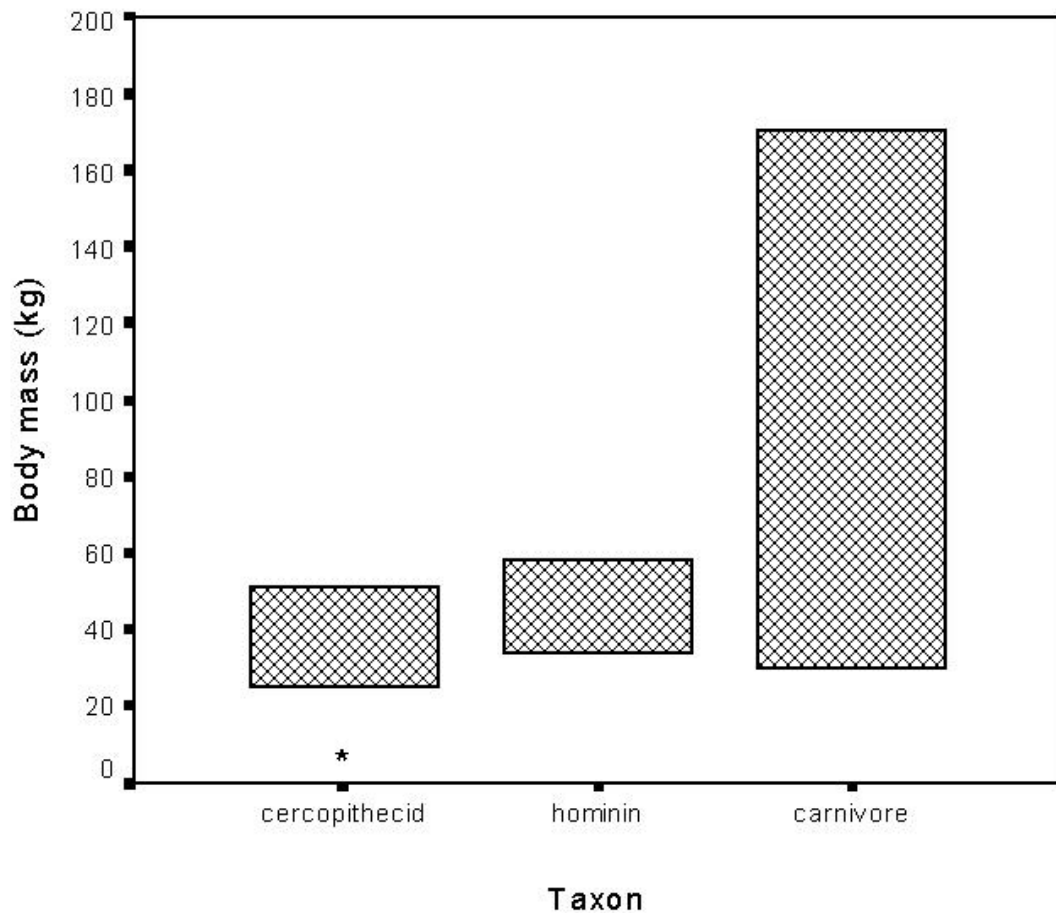


Figure 1: Probable body mass ranges of cercopithecoids, hominins and carnivores found in either or both the Upper Burgi and the KBS Members at Koobi Fora. Cercopithecoid taxa include *C. kimuei* (51kg), *T. oswaldi* (50kg) and *C. williamsi* (25kg) (Delson *et al.* 2000). The body mass estimate for *Cercopithecus* (see text) is represented by \*. Hominin taxa include *H. ergaster* (58kg), *P. boisei* (44kg) and *H. habilis* (34kg) (Wood & Collard 1999). Carnivore taxa include *Homotherium crenatidens* (170kg) and *Canis mesomelas* (30 kg) (taxon listing from Turner *et al.* 1999; body mass data from Plummer 2004).

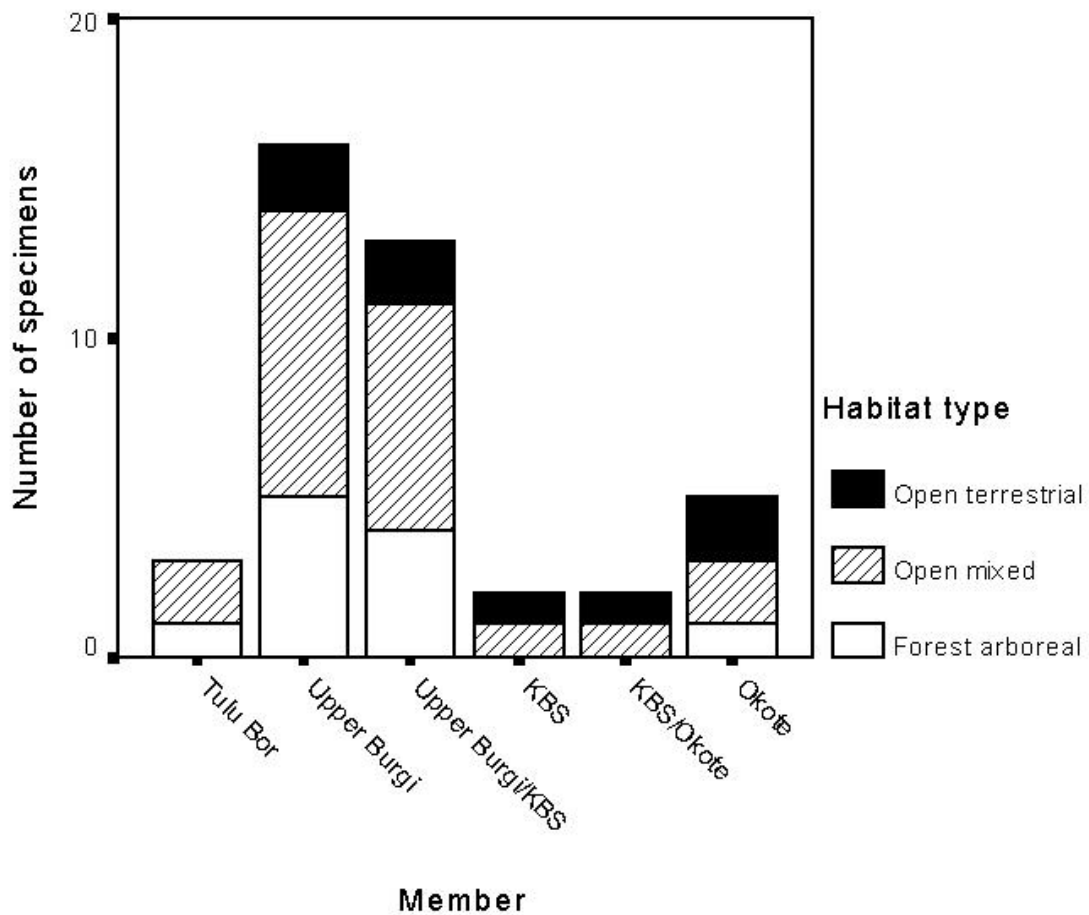


Figure 2: Habitat categories and locomotor preferences of cercopithecids from Koobi Fora.

Elements represented are proximal and distal humerus, proximal ulna and distal femur (after Elton, 2001, 2002). 'Open terrestrial' refers to cercopithecids that use terrestrial locomotion most of the time in open habitats. 'Open mixed' refers to cercopithecids that use terrestrial and arboreal locomotion in relatively open habitats. 'Forest arboreal' refers to cercopithecids that use arboreal locomotion in closed (forested) habitats (further details can be found in Elton 2001, 2002).

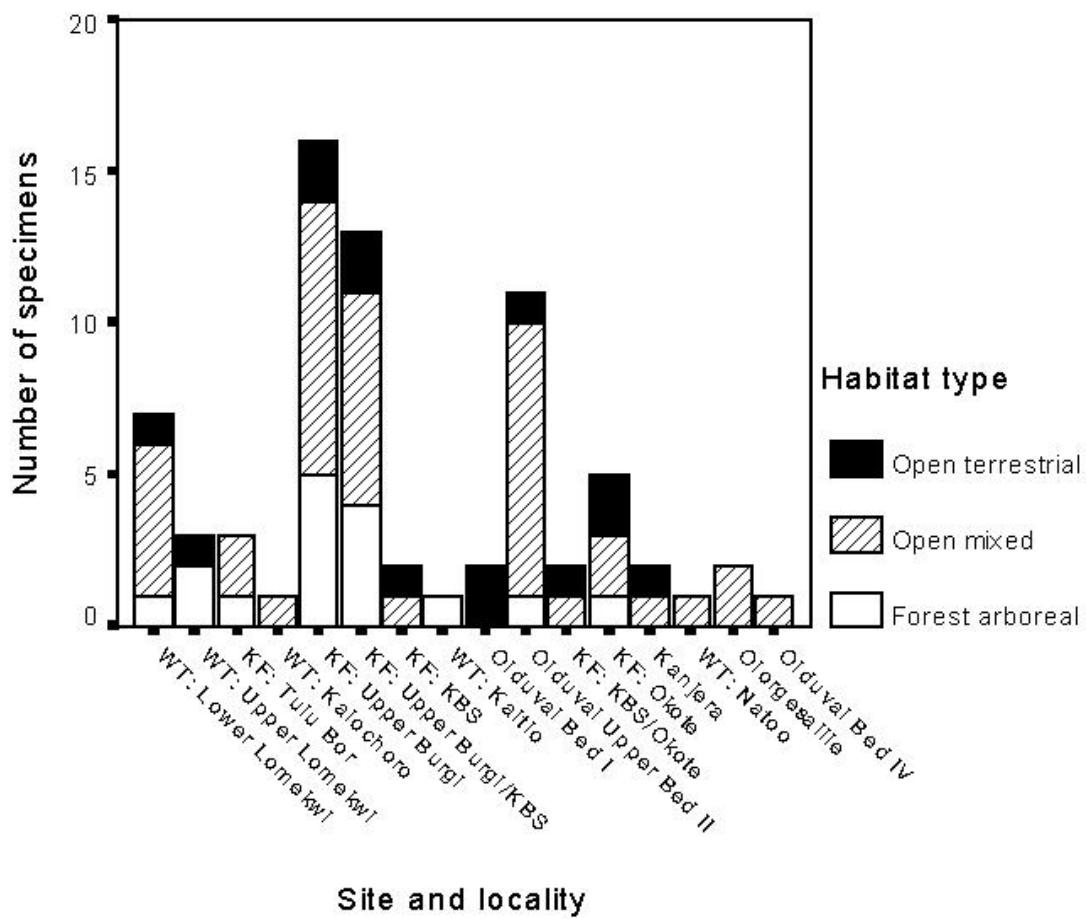


Figure 3: Habitat categories and locomotor preferences of cercopithecids from Plio-Pleistocene sites in East Africa. Elements represented are proximal and distal humerus, proximal ulna and distal femur (after Elton, 2001, 2002). WT: West Turkana; KF: Koobi Fora.



Figure 4: Schematic representation of the diets of Koobi Fora cercopithecids, hominins, suids and carnivores. Diets based on data from Wood & Strait (2004), Jolly (1972), Lee-Thorp *et al.* (1989), Benefit (1999), Bishop (1999).

